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Early and Late Modulation of Saccade Deviations by Target Distractor Similarity

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Submitted 22 January 2009; accepted in final form 15 June 2009

Mulckhuyse M, Van der Stigchel S, Theeuwes J. Early and late modulation of saccade deviations by target distractor similarity. *J Neurophysiol* 102: 1451–1458, 2009. First published June 24, 2009; doi:10.1152/jn.00068.2009. In this study, we investigated the time course of oculomotor competition between bottom-up and top-down selection processes using saccade trajectory deviations as a dependent measure. We used a paradigm in which we manipulated saccade latency by offsetting the fixation point at different time points relative to target onset. In *experiment 1*, observers made a saccade to a filled colored circle while another irrelevant distractor circle was presented. The distractor was either similar (i.e., identical) or dissimilar to the target. Results showed that the strength of saccade deviation was modulated by target distractor similarity for short saccade latencies. To rule out the possibility that the similar distractor affected the saccade trajectory merely because it was identical to the target, the distractor in *experiment 2* was a square shape of which only the color was similar or dissimilar to the target. The results showed that deviations for both short and long latencies were modulated by target distractor similarity. When saccade latencies were short, we found less saccade deviation away from a similar than from a dissimilar distractor. When saccade latencies were long, the opposite pattern was found: more saccade deviation away from a similar than from a dissimilar distractor. In contrast to previous findings, our study shows that task-relevant information can already influence the early processes of oculomotor control. We conclude that competition between saccadic goals is subject to two different processes with different time courses: one fast activating process signaling the saliency and task relevance of a location and one slower inhibitory process suppressing that location.

INTRODUCTION

Each time the eyes move, a point of interest in the visual field is selected as a saccadic goal. These points of interest are assumed to be represented in a topographic salience map that guides the saccadic target selection process (Findlay and Walker 1999; Itti and Koch 2000, 2001). In this map, salient objects in the environment may capture the eyes through a bottom-up selection process (Theeuwes et al. 1998). These bottom-up selection processes can compete strongly with a saccadic goal that is based on top-down selection processes. Top-down selection processes refer to the voluntary selection of a saccadic goal, for example, guided by knowledge of a specific color or shape. In visual search, competition between bottom-up and top-down selection processes is reflected by longer saccade latencies to a saccade target in the presence of a salient distractor, by the number of erroneous saccades to a

distractor, and by saccade trajectory deviations in the presence of a distractor (Godijn and Theeuwes 2002; Theeuwes and Godijn 2004; Van der Stigchel and Theeuwes 2005; Van der Stigchel et al. 2006). When bottom-up information becomes task relevant, for example, by increasing similarity between target and distractor, the top-down task relevant information integrates with the bottom-up saliency information. The combined information of task relevance and bottom-up saliency is represented in a so called priority map (Fecteau and Munoz 2006). These task relevant salient distractors are given priority by the oculomotor system. As a result, the competition between salient distractors that are in addition task relevant and top-down target goals becomes stronger. In visual search, this is reflected by longer saccade latencies in the presence of a similar distractor compared with a dissimilar distractor, by more erroneous saccades to a similar distractor compared with a dissimilar distractor, and by longer fixation durations on a similar distractor than on a dissimilar distractor (Ludwig and Gilchrist 2002, 2003a; Mulckhuyse et al. 2008). The aim of this study is to investigate the time course of competition between bottom-up and top-down selection processes using saccade trajectory deviation as the dependent measure.

Saccade trajectory deviations refer to the modulation of saccade trajectory in the presence of competing stimuli (for review, see Van der Stigchel et al. 2006; Walker and McSorley 2008) and can deviate towards or away from the competing stimulus. Saccade deviations are explained by a neural map in which distractor and target location both evoke activity. Saccade direction within this map is encoded by populations of neurons with broad and overlapping receptive fields. The initial activity at the target and distractor location is averaged, and as a consequence, the saccade trajectory deviates towards the distractor (McPeck 2006; McPeck et al. 2003). Saccade deviations away from distractors are believed to result from an additional inhibitory process (Doyle and Walker 2001, 2002; McSorley et al. 2004; Sheliga et al. 1994, 1995, 1997; Tipper et al. 2001; Walker et al. 2006). If the distractor-related activity is inhibited below a baseline level, the average result will be negative. As a consequence, the saccade trajectory will deviate away from the distractor location (Van der Stigchel et al. 2006; Walker and McSorley 2008).

Neural correlates of saccade target selection and saccade trajectory deviations are found in the superior colliculus (SC) and the frontal eye fields (FEFs) (McPeck 2006; McPeck and Keller 2002; McPeck et al. 2003). In nonhuman primates, the SC and the FEF are part of the network for saliency mapping (Munoz 2002; Schall and Thompson 1999; Thompson and Bichot 2005). This network also includes the lateral intrapari-

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atal area (LIP; Kusunoki et al. 2000) that projects to the FEF and the intermediate layers of the SC (Munoz and Everling 2004), but activity in LIP is independent of saccade generation and saccade execution (Colby and Goldberg 1999; Gottlieb et al. 1998). McPeck et al. (2003) recorded activity of neurons in the SC and found an association between saccade deviation towards a distractor and enhanced activity at the distractor location just before saccade initiation. In addition, subthreshold electrical microstimulation in the SC immediately before saccades to single targets produced saccades that deviated towards the location coded by the stimulated site. McPeck et al. suggested that ongoing competition between target and distractor stimuli are associated with saccade deviation towards the distractor. More recently, McPeck (2006) found a similar pattern of neural activity in the FEF, i.e., enhanced activity just before saccade initiation was associated with saccade deviation towards.

Although saccade deviation towards has been shown in monkeys and humans (Walker et al. 2006), saccade deviation away has been shown in humans only (Van der Stigchel et al. 2006). In one of the classic studies on saccade deviations (Sheliga et al. 1994, 1995, 1997), saccade trajectories deviated away from a previously attended location. For instance, in one of these studies (Sheliga et al. 1994), participants had to attend to a cue that indicated the subsequent oculomotor behavior. This cue was presented within one of four peripheral boxes positioned in the upper or lower visual field and to the left or right of the target locations. Results showed that the eyes deviated away from the imperative stimulus that was previously attended, indicating that covert spatial attention also affects saccade trajectories.

Previous research studying the competition between bottom-up and top-down selection processes has shown that saccades with short latencies tend to deviate towards distractors, whereas saccades with longer latencies tend to deviate away from distractors (Godijn and Theeuwes 2002; McSorley et al. 2006; Theeuwes and Godijn 2004). McSorley et al. (2006), for instance, manipulated saccade latency by using a fixation gap paradigm (Saslow 1967): the longer the gap between fixation offset and target onset, the shorter the saccade latencies will be. In contrast, the shorter the gap—or the longer the overlap between fixation offset and target onset—the longer the saccade latencies will be. In the study of McSorley et al., subjects made saccades to a target that could appear at one of four possible locations while a distractor was presented simultaneously. The results showed basically a linear relationship between saccade latency and saccade deviation: saccade with short latencies deviated towards the distractor, whereas saccades with long latencies deviated away from the distractor. The authors suggested that two separate neural mechanisms are responsible for the different directions of deviation. In their view, deviation towards a distractor is the result of a fast feed-forward process without top-down inhibition. The initial decrease in deviation towards a distractor reflects the local competitive inhibition processes between target and distractor locations in the neural map (Port and Wurtz 2003). The neural mechanism that causes deviation away from a distractor is a second slower top-down inhibitory process suppressing distractor-related activity in the neural map.

Ludwig and Gilchrist (2003b) found that the stronger competition between distractor and target modulated exclusively

this latter inhibitory process. In their study, subjects had to make an eye movement to a no-onset target along the vertical meridian while an onset distractor was presented on the horizontal meridian. The color of the onset distractor was either similar or dissimilar to the target. Results showed that saccade latencies increased in the presence of a similar distractor relative to a dissimilar distractor, but the similar distractor modulated the saccade trajectory only late in time: when the onset of the distractor preceded the target display or when saccade initiation was delayed because of a continuous fixation point. Only under these conditions stronger deviation away from the similar distractor relative to a dissimilar distractor was observed. Ludwig and Gilchrist concluded that distractor related activity is initially bottom-up driven, whereas later in time, additional top-down signals (such as task relevant color information) can enhance the distractor related activity. They explained their results by claiming that early in time, resolving the competition between target and distractor-related activity requires less suppression than later in time, because not until later in time top-down activity of the color being relevant becomes available. In other words, only later in time, the task relevant color information enhances the distractor-related activity. However, in Ludwig and Gilchrist, the mean saccade latencies were all well above 200 ms, which is believed to be the point in time where saccade deviation toward a distractor turns to saccade deviation away from a distractor (McSorley et al. 2006, 2009; Theeuwes and Godijn 2004). Because of these relatively long saccade latencies, it is possible that they could only show the late modulation reflecting the suppression of a distractor that was similar to the target but not the early modulation reflecting the enhancement of that same distractor.

In this study, we investigated whether top-down information relevant for the task at hand can influence the oculomotor system early in time, that is, before inhibitory processes start playing a role. To this end, we used the fixation gap and overlap paradigm (McSorley et al. 2006; Saslow 1967) to induce both short and long saccade latencies. The onset distractors could either be similar or dissimilar to the target and were presented to the left or the right of the target. Target locations were indicated by placeholders on the vertical meridian. We expected to find an effect of saccade latency on saccade deviation: deviation towards the distractor for shorter saccade latencies and deviations away from the distractor for longer saccade latencies. Furthermore, we expected that saccade deviation would be modulated by target distractor similarity.

METHODS

Experiment 1

PARTICIPANTS. Twelve paid volunteers (18–24 yr of age) participated in the experiment. All participants had normal or corrected to normal vision.

The protocol was approved by the Ethical Committee of the VU, Amsterdam, The Netherlands.

APPARATUS AND DESIGN. A Pentium IV computer with a processor speed of 2.3 GHz controlled the timing of the events. Displays were presented on an Iiyama 21-in SVGA monitor with a resolution of $1,024 \times 768$ pixels and a 100-Hz refresh rate. A second computer controlled the registration of eye movement's data on-line. Eye movements were registered by means of a video-based eye tracker

(SR Research). The Eyelink 1000 Tower Mount system has a 1,000-Hz temporal resolution, $<0.01^\circ$ of gaze resolution (noise limited), and gaze position accuracy of $<0.5^\circ$. Data from the left eye were monitored and analyzed. The distance between monitor and chin rest was 70 cm. The experiment was conducted in a sound-attenuated and dimly lit room.

The experiment consisted of two blocks: one block without a distractor (baseline condition) and one block with a distractor, either similar (similar distractor condition) or dissimilar (dissimilar distractor condition) to the target. In addition, during both blocks, the fixation cross was removed at five different stimulus onset asynchronies (SOAs) of -150 , -50 , 0 , 50 , or 150 ms relative to target onset. In total, each of the distractor conditions consisted of 400 trials, 80 trials for each of the five gap intervals. The baseline condition consisted of 200 trials, 40 trials for each of the five gap intervals. Trials were randomly distributed throughout a block. The target appeared equally often above or below the fixation point. One half of the participants started with the baseline block and the other half with the distractor block.

All stimuli were presented on a black background. Two possible target locations, 7.73° above and below fixation point at the center of the display, were indicated by filled gray ($x = 0.279$, $y = 0.312$) circles of 1.23° . An equiluminant color change of one of these gray circles indicated the saccadic target location. One half of the subjects made a saccade to a red circle target ($x = 0.519$, $y = 0.332$) and the other half to a green circle target ($x = 0.285$, $y = 0.533$). In the distractor conditions, an onset distractor, either red or green, was presented at the moment of target onset, either to the left or to the right of fixation in the same upper or lower visual field as the target. These conditions were randomized within a block. The vertical distance of the distractor from fixation was 5.31° ; the horizontal distance of the distractor from fixation was 6.52° . All colors were matched for luminance (14 cd/m^2). Figure 1A shows the sequence of a trial in the similar distractor condition with a fixation offset before target onset.

PROCEDURE. Before the experiment started, the Eyelink 1000 system was calibrated. Participants had to fixate nine calibration targets that were presented randomly in a 3×3 grid across the monitor. On each trial in the experiment, participants were instructed to fixate the center fixation point and to press the space bar to recalibrate the position of the eyes. The fixation point changed into a plus sign as an indication that the positions of the eyes were recalibrated.

Participants were told to make a saccade to the saccadic target. To avoid anticipation saccades, a warning beep was presented when participants responded too fast (<80 ms). The warning beep was also presented when participants responded too slow (>600 ms). Participants started each block with 20 practice trials.

DATA ANALYSIS. A saccade was defined as a correct saccade if the starting position was within 1° of horizontal distance and within 2° of

vertical distance from the center fixation point. Furthermore, the initial saccade was assigned to a target if the endpoint of the initial saccade was within 3° of the center of the target position and to a distractor if the endpoint was within 3° of the center of the distractor position. Saccade latencies <80 ms or >600 ms were excluded from analyses. Latencies shorter or longer than 2.5 SD away from the mean latency were also excluded. Moreover, too small saccades ($<3^\circ$) were excluded from analyses.

Saccade trajectories were examined by calculating the mean angle of the actual saccade path relative to the mean angle of a straight line between the starting point of the saccade and the saccadic target. The angle of the actual saccade was calculated for each 2-ms sample point by examining the angle of the straight line between fixation and the current sample point. Angles were averaged across the whole saccade and subtracted from the angle of the straight line between fixation and the target location (for a more detailed overview of saccade trajectory computation, see Van der Stigchel et al. 2006). To compute the influence of the distractor on saccade trajectories, we compared each saccade in a trial with a distractor to that of the averaged mean path angles of all trials without a distractor, to determine whether the saccade in the presence of a distractor deviated towards or away from the location of the distractor. Deviations were signed so that a positive value indicated deviation towards the distractor and a negative value deviation away. All deviations are given in radians.

Experiment 2

PARTICIPANTS. Twelve paid volunteers (18–24 yr of age) participated in the experiment. All participants had normal or corrected to normal vision.

APPARATUS AND DESIGN PROCEDURE AND DATA ANALYSES. The procedure was the same as in *experiment 1* with the exceptions that distractor absent and distractor present trials were mixed within a block and that the distractor was a filled square (1.06° on each side) instead of a filled circle. The filled square either had the same color as the filled target circle (similar condition) or had a different color (dissimilar condition). Figure 1B shows the sequence of a trial in the similar distractor condition with a fixation offset before target onset.

RESULTS

Experiment 1

Based on the criteria described above, 15.8% of the trials in the similar condition were excluded from analyses: 13.7% in the dissimilar condition and 14.3% in the baseline condition. A Friedman test on percentage of errors showed that there was no difference between the three conditions.

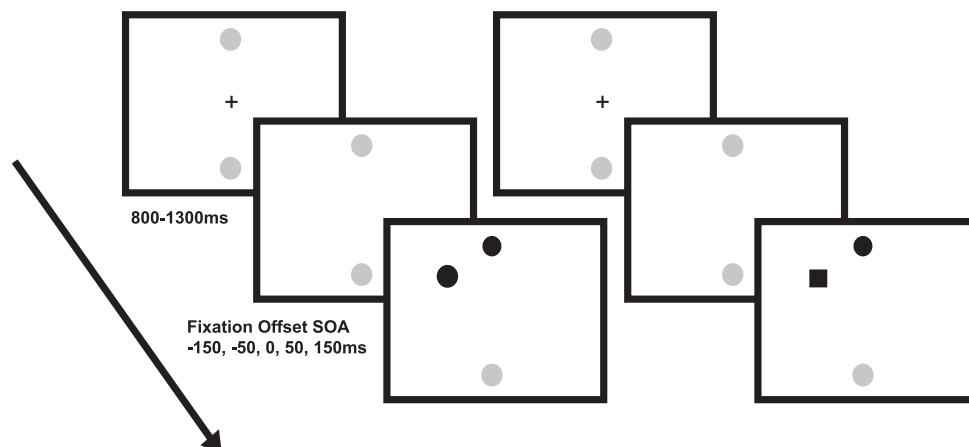


FIG. 1. A: from top to bottom, succession of events in a trial in *experiment 1* in which the target and distractor have the same color and shape. Fixation point offset occurred before target onset. B: from top to bottom, succession of events in a trial in *experiment 2* in which the target and distractor have the same color but not the same shape. Fixation point offset occurred before target onset.

SACCADE DIRECTION. In the similar condition, 4.7% of all initial saccades ended on the distractor, and in the dissimilar condition, 1.8% of all initial saccades ended on the distractor. A two-related Wilcoxon test was significant ($Z = 2.986$, $N\text{-ties} = 12$, $P < 0.01$), showing that the similar distractor captured the eyes more often than the dissimilar distractor.

SACCADE LATENCY. Figure 2 shows the mean saccade latency for each condition per fixation offset SOA. As can be seen, fixation offset SOA influenced saccade latencies. A repeated-measures ANOVA with condition (baseline, dissimilar distractor, and similar distractor) and fixation offset SOA as factors showed a main effect of fixation offset SOA [$F(4,44) = 123.641$, $P < 0.01$, with Greenhouse–Geisser correction]. The earlier the fixation offset before target onset, the shorter the saccade latencies in each condition ($P < 0.01$). Similar, the later the fixation offset after target onset, the longer saccade latencies in each condition ($P < 0.01$). This pattern of results is similar to McSorley et al. (2006) and indicates that the fixation gap manipulation was successful in generating both short and long saccade latencies within one paradigm. In addition to the main effect, we found an interaction between fixation offset SOA and condition [$F(8,88) = 7.487$, $P < 0.01$, with Greenhouse–Geisser correction].

To examine the effect of saccade latency on saccade deviation, the latency distribution for each subject and for each distractor condition was divided into five bins. Figure 3 shows the mean saccade latency per bin per distractor condition. An ANOVA with condition (dissimilar distractor and similar distractor) and bin as factors showed a main effect of condition [$F(1,11) = 6.492$, $P < 0.05$]. Planned comparisons showed that the main effect of condition was caused by significant shorter saccade latencies in the dissimilar distractor condition compared with the similar condition in the first [$t(11) = 2.341$, $P < 0.05$], the second [$t(11) = 4.458$, $P < 0.01$], and the third bin [$t(11) = 3.717$, $P < 0.01$]. This is consistent with previous research (Ludwig and Gilchrist 2003a,b; Mulckhuyse et al. 2008) in which shorter saccade latencies were found in the presence of a dissimilar distractor compared with a similar distractor. The absence of an interaction between bin and condition ($F = 1.79$) indicates that the effect of target distrac-

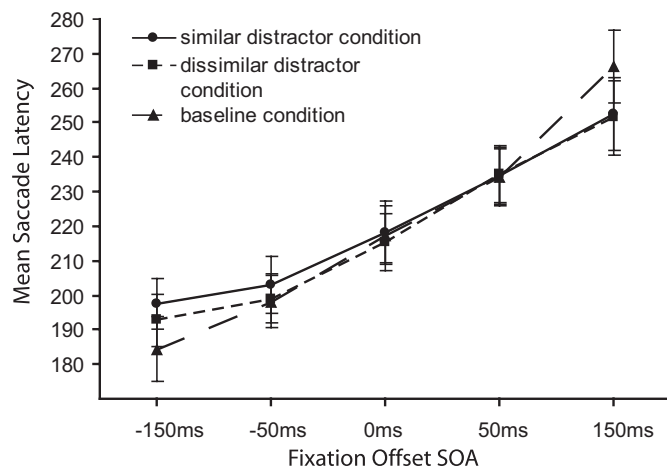


FIG. 2. Mean saccade latency in *experiment 1* for the similar distractor (●), dissimilar distractor (■), and baseline (▲) condition per fixation offset stimulus onset asynchrony (SOA; -150, -50, 0, 50, 150).

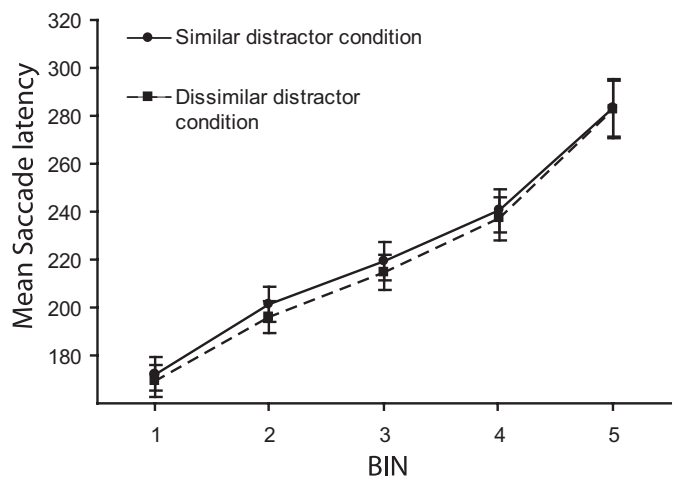


FIG. 3. Mean saccade latency in *experiment 1* for the similar distractor (●) and dissimilar distractor (■) condition per bin.

tor similarity on saccade latency was independent of the effect of bin on saccade latency.

SACCADE DEVIATION. Figure 4 shows the mean saccade deviation per condition per bin and mean saccade latency per condition per bin. As can be seen, target distractor similarity had an effect on saccade deviation. An ANOVA on saccade deviation with condition (similar and dissimilar) and bin as factors showed a significant main effect of bin [$F(4,44) = 6.213$, $P < 0.05$, with Greenhouse–Geisser correction]. More importantly, however, the interaction between condition and bin was highly significant [$F(4,44) = 4.194$, $P < 0.01$]. Post hoc comparisons showed that saccade deviations in the first and second bins differed significantly between the two conditions: in the first bin, target distractor similarity modulated saccade deviations in such a way that the saccades in the similar distractor condition deviated toward the distractor, whereas saccades in the dissimilar distractor condition deviated away from the distractor [$t(11) = 2.968$, $P < 0.05$]. In the second bin, saccades deviated away from the distractor in both conditions but less so in the similar distractor condition compared with the dissimilar distractor condition [$t(11) = 3.981$, $P < 0.01$]. In addition to the target distractor similarity effect on saccade deviation, a one-sample t -test showed that in the

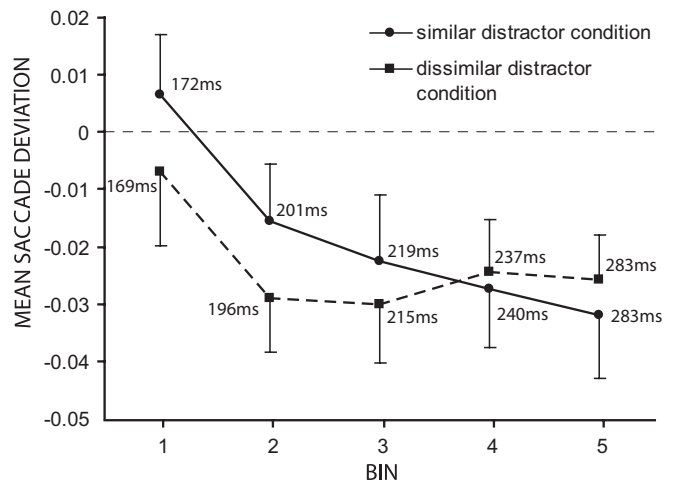


FIG. 4. Mean saccade deviation and mean saccade latency in *experiment 1* for the similar distractor (●) and dissimilar distractor (■) condition per bin.

similar distractor condition saccades deviated away significantly from zero in the last two bins ($P < 0.05$) and in the dissimilar condition the saccades deviated away significantly from zero in all but the first bin ($P < 0.05$).

Experiment 2

Based on the criteria described above, 16.2% of the trials in the similar condition were excluded from analyses: 16.3% in the dissimilar condition and 17.3% in the baseline condition. A Friedman test on percentage of errors showed that there was no difference between these conditions.

SACCADIC DIRECTION. In the similar condition, 2.9% of initial saccades ended on the distractor, and in the dissimilar condition, 1.2% of initial saccades ended on the distractor. A two-related Wilcoxon test was significant ($Z = 2.866$, N -ties = 12, $P < 0.01$), showing that the similar distractor captured the eyes more often than the dissimilar distractor.

SACCADIC LATENCY. A repeated-measures ANOVA with condition (baseline, dissimilar distractor, and similar distractor) and fixation offset SOA as factors showed a main effect of fixation offset SOA [$F(4,44) = 78.329$, $P < 0.01$, with Greenhouse–Geisser correction]. As seen in Fig. 5, the earlier the fixation offset before target onset, the shorter the saccade latencies in each condition ($P < 0.01$). Similar, the later the fixation offset after target onset, the longer saccade latencies in each condition ($P < 0.01$). This pattern of results is similar to *experiment 1* and again confirms that the fixation gap manipulation was successful in generating both short and long saccade latencies within one paradigm. In addition to the main effect, we found an interaction between fixation offset SOA and condition [$F(8,88) = 3.327$, $P < 0.05$, with Greenhouse–Geisser correction] and a main effect of condition [$F(2,22) = 6.1$, $P < 0.05$, with Greenhouse–Geisser correction]. The mean saccade latency in the dissimilar condition was significantly shorter than the mean saccade latency in the similar condition ($P < 0.05$), and the mean saccade latency in the similar condition was significantly shorter than the mean saccade latency in the baseline condition ($P < 0.01$).

To examine the effect of saccade latency on saccade deviation, the latency distribution for each subject and for each

distractor condition was divided into five bins. An ANOVA with condition (dissimilar distractor and similar distractor) and bin as factors showed a main effect of condition [$F(1,11) = 11.166$, $P < 0.01$]. Planned comparisons showed that the main effect of condition was caused by significant shorter saccade latencies in the dissimilar distractor condition compared with the similar condition in all but the last bin ($P < 0.05$). As Fig. 6 shows, the absence of an interaction between bin and condition ($F < 1$) indicates that the effect of target distractor similarity on saccade latency was independent of the effect of bin on saccade latency. These results are consistent with the results obtained in *experiment 1*.

SACCADIC DEVIATION. Figure 7 shows the mean saccade deviation per condition per bin and mean saccade latency per condition per bin. As can be seen, target distractor similarity had a clear effect on saccade deviation for the short and the long latencies. An ANOVA on saccade deviation with condition (similar or dissimilar) and bin as factors showed a significant main effect of bin [$F(4,44) = 6.128$, $P < 0.01$, with Greenhouse–Geisser correction]. Replicating *experiment 1*, the interaction between condition and bin was significant [$F(4,44) = 3.266$, $P < 0.05$]. Post hoc comparisons showed that saccade deviations in the first and the last bin differed significantly between the two conditions. In the first bin, target distractor similarity modulated the saccade deviations in such a way that the saccades deviated less away from the similar distractor than from the dissimilar distractor [$t(11) = 1.940$, $P < 0.05$, 1-tailed]. The last bin showed exactly the opposite pattern: saccades deviated away more from the similar distractor than from the dissimilar distractor [$t(11) = 2.150$, $P < 0.05$, 1-tailed]. In addition to the target distractor similarity effect on saccade deviation, a one-sample t -test showed that, in the similar distractor condition, saccades deviated away significantly from zero in the last three bins ($P < 0.05$), whereas in the dissimilar condition, saccades already deviated away significantly from the first bin ($P < 0.05$).

DISCUSSION

Experiment 1

Results showed that saccade latency affected saccade deviation and, in addition, this effect was modulated by target distractor similarity. For the short latencies, saccades in the similar distractor condition tended to deviate towards a distractor, whereas saccades in the dissimilar distractor condition already tended to deviate away from a distractor. At longer saccade latencies, saccades deviated away from the distractor in both conditions and were no longer modulated by target distractor similarity. These results are not consistent with the results obtained by Ludwig and Gilchrist (2003b). In contrast to our findings, they found that modulation of saccade deviations by target distractor similarity occurs only late in time. Ludwig and Gilchrist explained their results by claiming that only later in time did the task relevant color information enhance the distractor-related activity, which in turn resulted in stronger suppression. Our results suggest that, early in time, task relevant color signals enhance distractor-related activity in such a way that suppression has not yet been accomplished.

However, it is possible that our findings can be explained by other factors than the enhancement of distractor-related activity

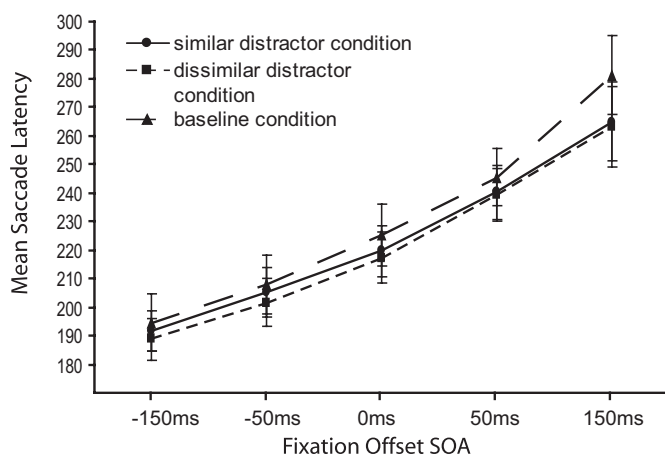


FIG. 5. Mean saccade latency in *experiment 2* for the similar distractor (●), dissimilar distractor (■), and baseline (▲) condition per fixation offset SOA (−150, −50, 0, 50, 150).

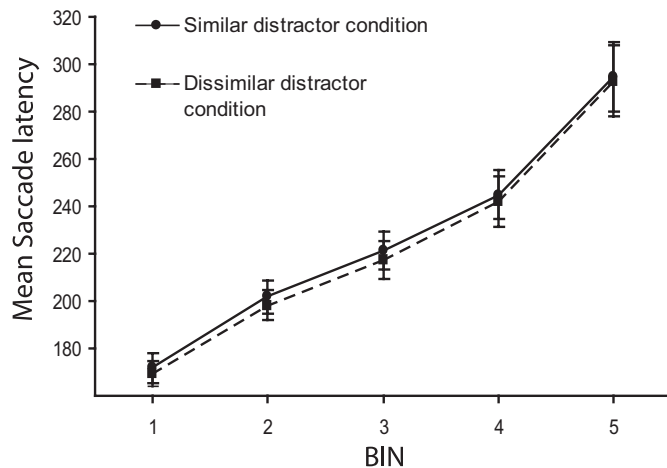


FIG. 6. Mean saccade latency in *experiment 2* for the similar distractor (●) and dissimilar distractor (■) condition per bin.

caused by task relevant signals. Even though the distractor was always presented at a different location than the target, the distractor had the same color and shape as the target. It is feasible that, in this condition, saccades deviated more towards the distractor not so much because of target-distractor similarity per se but more because observers were confused about what the target and what the distractor was. Note that, in the similar condition, the target could only be distinguished from the distractor on the basis of location. In *experiment 2*, we ensured the shape of the distractor was clearly different from the target and thus could be distinguished on the basis of the feature shape. Whereas in *experiment 1*, both target and distractor were filled colored circles, in *experiment 2*, the target was always a filled colored circle, whereas the distractor was always a filled colored square. Previous research has shown that observers can easily distinguish a circle from a square (Theeuwes 1992).

In *experiment 2*, we addressed another potential concern. In *experiment 1*, we presented distractor present and absent conditions in a blocked fashion, allowing different search strategies between experimental and control conditions. Notably, it has been shown that the mere expectation of a distractor can already cause saccades to deviate away from a distractor location (Van der Stigchel and Theeuwes 2006). To prevent anticipation of the distractor, we presented distractor present and absent trials mixed within a block of trials.

Experiment 2

Experiment 2 shows the same pattern of results as *experiment 1*; saccade latency affected saccade deviation, and in addition, this effect was modulated by target distractor similarity. At short latencies, saccades in the similar distractor condition deviated less away from the distractor than saccades in the dissimilar distractor condition. In contrast, at long latencies, saccades deviated away more from the distractor in the similar condition than in the dissimilar condition. The latter result is consistent with the results obtained by Ludwig and Gilchrist (2003b) and shows the stronger inhibitory processes necessary to inhibit the stronger enhancement of the distractor-related activity when the distractor is similar to the target. The early modulation of saccade deviation shows that the similar

distractor is not yet suppressed, whereas the dissimilar distractor already is. This is also evident from the finding that the saccades in the dissimilar condition deviated away from zero significantly from the first bin on, whereas the saccades in the similar condition did not significantly deviate away from zero until the third bin.

General discussion

The aim of this study was to investigate the time course of competition between bottom-up and top-down selection processes using saccade trajectory deviations as the dependent measure. Results showed that saccade latency affected saccade deviation and, in addition, this effect was modulated by target distractor similarity.

At short latencies, saccade deviations in the presence of a similar distractor were not suppressed or less suppressed than saccade deviations in the presence of a dissimilar distractor. Furthermore, in both experiments, saccades in the dissimilar distractor condition deviated away from zero before saccades in the similar distractor condition started to deviate away from zero. Because it is assumed that deviation away represents suppression in the oculomotor system (Van der Stigchel et al. 2006), these results indicate that suppression of a distractor dissimilar to the target is accomplished before a distractor similar to a target is suppressed. Early suppression of a dissimilar distractor may possibly be resolved through local inhibitory processes between target and distractor locations. The slower additional top-down inhibitory process suppressing distractor related activity is manifested later in time (McSorley et al. 2006). In both experiments, saccades deviated away more strongly from the distractor at long latencies compared with short latencies and, in addition, these deviations were modulated by target distractor similarity in *experiment 2*. The reason why we did not find target distractor modulations at long saccade latencies in *experiment 1* could be explained by the difference in search strategies. In *experiment 2*, distractor present and distractor absent trials were mixed and therefore observers may have asserted less inhibition of the potential distractor locations before a trial started. When observers were unable to anticipate a distractor, there was more suppression

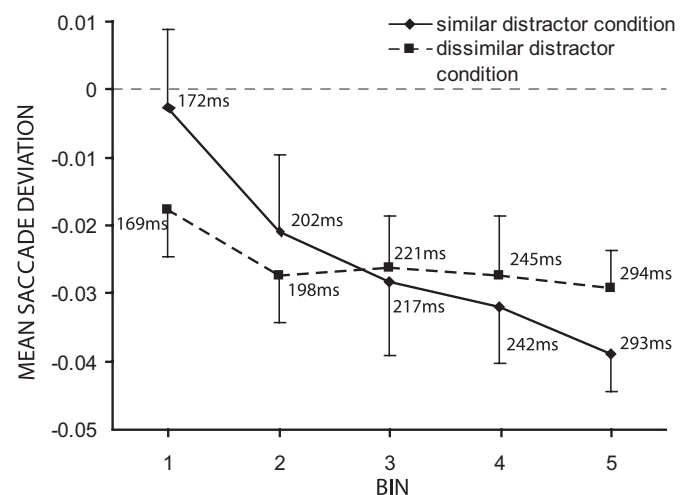


FIG. 7. Mean saccade deviation and mean saccade latency in *experiment 2* for the similar distractor (●) and dissimilar distractor (■) condition per bin.

(i.e., more deviation away) of a similar than a dissimilar distractor.

This latter result is consistent with Ludwig and Gilchrist (2003b). However, their conclusion that task relevant color information enhances the distractor-related activity late in time does not seem to be consistent with our results. Early in time, saccade trajectories were already affected by whether the color of the distractor was task relevant or not. In their paper, Ludwig and Gilchrist do, however, note that it would be paradoxical to assume that task-related information (i.e., the target color) would not be available to the saccadic system early in time because the endpoint of the saccade is selected on the basis of color information. They explained this paradox by the small number of possible target locations (2) in their study. In their view, a limited number of possible target locations requires only a small amount of sensory evidence for the saccadic system to select that location. In other words, they claimed that the task-related color information was not yet fully processed, neither at the target location nor at the distractor location at the time of saccade initiation. Although we agree that limiting the number of possible target locations may have an effect on distractor processing, our results indicate that color information was processed at the time of saccade initiation, as shown by the early modulation of saccade deviation. One explanation for the different findings between Ludwig and Gilchrist and our study is the difference in paradigms. Because we used a fixation offset procedure, our saccades were initiated faster than those in their study. It is possible that the early modulation of the saccade deviation dependent on target distractor similarity only shows up when saccades can be generated very quickly.

Several studies investigating the neural basis of saccade target selection with nonhuman primates showed that neurons in the FEF are modulated by activation based on target distractor similarity in visual search (Bichot 2001; Thompson et al. 2005). Bichot and Schall (1999), for instance, showed that, after an initial nonselective response, distractors similar to the target elicited higher activity in the FEF than distractors dissimilar to the target. Higher activation within the FEF (McPeck 2006) and within the SC (McPeck et al. 2003) before saccade onset is associated with stronger deviation toward distractors. It is possible that enhanced activity in the FEF, signaling the priority of the location because of its task relevance, causes the modulation of saccade deviation early in time. Possibly this fast activating process is transferred via the direct connection from the FEF to the SC (Schlag-Rey et al. 1992; Sommer and Wurtz 2000). Subsequently, because of the enhanced activity at the distractor location, stronger inhibition is necessary to resolve the competition between distractor and target (see also Ludwig and Gilchrist 2003b). Consistent with this idea, we found more deviation away from the similar distractor than from the dissimilar distractor later in time. In line with the suggestion by McSorley et al. (2006), this additional inhibitory signal seems to reach the neural map after 200 ms. The indirect inhibitory signal (Hikosaka and Wurtz 1983; McHaffie et al. 2005) from the FEF to the SC could be responsible for this later suppression.

How can we reconcile these findings showing an early top-down modulation of saccade trajectories given the generally accepted view that early saccades are basically driven by bottom-up salience only (Donk and van Zoest 2008; Godijn

and Theeuwes 2002; Ludwig and Gilchrist 2002, 2003a, b; Mulckhuyse et al. 2008; van Zoest and Donk 2005, 2006; van Zoest et al. 2004)? We assume that bottom-up salience and top-down information signals integrate in a spatiotopic saccade map (Findlay and Walker 1999; Godijn and Theeuwes 2002; Kopecz 1995; Trappenberg et al. 2001). According to this idea, saccadic target selection is initially based on bottom-up salience information. After the initial bottom-up activity, top-down influences can enhance or inhibit this activation. In this study, the saccadic target goal—an equiluminant color change—was presented simultaneously with the distractor—an onset. It is assumed that, because of its bottom-up salience, the presentation of the distractor results in a quick build up of activation in the saccade map at the location of the distractor. Therefore the onset of the distractor may have captured attention in a bottom-up fashion in at least a subset of the trials (Mulckhuyse et al. 2008; Theeuwes 1992; Theeuwes and Van der Burg 2007). When the distractor is dissimilar from the target, the subsequent suppression of the distractor location is rather fast. This inhibitory process may be accomplished through local inhibition: enhanced activity at one location in the saccade map inhibits more distant locations (Godijn and Theeuwes 2002). In this study, top-down task relevant information enhancing target-related activity in the map may have initially been sufficient to inhibit the dissimilar distractor location. However, the similar distractor shared task relevant features with the target and, as a consequence, the task relevant information may have also enhanced the distractor location. Therefore slower top-down inhibitory processes are necessary to resolve the competition. In terms of attentional allocation, we assume that once attention is captured by the onset distractor, it takes longer to disengage attention from that location when the distractor is similar to the target than when the target is dissimilar to the target (Mulckhuyse et al. 2008; Theeuwes et al. 2003). In this study, the longer disengagement of attention from a distractor is also shown by the longer saccade latencies in the similar distractor condition compared with the dissimilar distractor condition (see Ludwig and Gilchrist 2003b; Mulckhuyse et al. 2008 for similar results). In other words, in the latter condition, we assume that it takes more time to decide that the distractor is not the target. Although the neural correlates of the mechanisms remain unclear, we conclude that competition between saccadic goals is subject to two different processes with different time courses: one fast activating process signaling the priority of a location, i.e., the saliency and task relevance, and one slower inhibitory process suppressing that location.

GRANTS

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REFERENCES

- Bichot NP.** Neural mechanisms of top-down selection during visual search. Presented at the 23rd Annual International Conference of the IEEE Engineering in Medicine and Biology Society, Istanbul, Turkey, October 25–28, 2001.
- Bichot NP, Schall JD.** Effects of similarity and history on neural mechanisms of visual selection. *Nat Neurosci* 2: 549–554, 1999.
- Colby CL, Goldberg ME.** Space and attention in parietal cortex. *Annu Rev Neurosci* 22: 319–349, 1999.
- Donk M, van Zoest W.** Effects of salience are short-lived. *Psych Sci* 19: 733–739, 2008.

- Doyle M, Walker R. Curved saccade trajectories: voluntary and reflexive saccades curve away from irrelevant distractors. *Exp Brain Res* 139: 333–344, 2001.
- Doyle MC, Walker R. Multisensory interactions in saccade target selection: curved saccade trajectories. *Exp Brain Res* 142: 116–130, 2002.
- Fecteau JH, Munoz DP. Saliency, relevance, and firing: a priority map for target selection. *Trends Cogn Sci* 10: 382–390, 2006.
- Findlay JM, Walker R. A model of saccade generation based on parallel processing and competitive inhibition. *Behav Brain Sci* 22: 661–721, 1999.
- Godijn R, Theeuwes J. Programming of endogenous and exogenous saccades: evidence for a competitive integration model. *J Exp Psychol Hum Percept Perform* 28: 1039–1054, 2002.
- Gottlieb JP, Kusunoki M, Goldberg ME. The representation of visual saliency in monkey parietal cortex. *Nature* 391: 481–484, 1998.
- Hikosaka O, Wurtz RH. Visual and oculomotor functions of monkey substantia nigra pars reticulata. 4. Relation of substantia nigra to superior colliculus. *J Neurophysiol* 49: 1285–1301, 1983.
- Itti L, Koch C. A saliency-based search mechanism for overt and covert shifts of visual attention. *Vision Res* 40: 1489–1506, 2000.
- Itti L, Koch C. Computational modelling of visual attention. *Nat Rev Neurosci* 2: 194–203, 2001.
- Kopeck K. Saccadic reaction-times in gap overlap paradigms - a model-based on integration of intentional and visual information on neural, dynamic fields. *Vision Res* 35: 2911–2925, 1995.
- Kusunoki M, Gottlieb J, Goldberg ME. The lateral intraparietal area as a saliency map: the representation of abrupt onset, stimulus motion, and task relevance. *Vision Res* 40: 1459–1468, 2000.
- Ludwig CJH, Gilchrist ID. Stimulus-driven and goal-driven control over visual selection. *J Exp Psychol Hum Percept Perform* 28: 902–912, 2002.
- Ludwig CJH, Gilchrist ID. Goal-driven modulation of oculomotor capture. *Percept Psychophys* 65: 1243–1251, 2003a.
- Ludwig CJH, Gilchrist ID. Target similarity affects saccade curvature away from irrelevant onsets. *Exp Brain Res* 152: 60–69, 2003b.
- McHaffie JG, Stanford TR, Stein BE, Coizet W, Redgrave P. Subcortical loops through the basal ganglia. *Trends Neurosci* 28: 401–407, 2005.
- McPeck RM. Incomplete suppression of distractor-related activity in the frontal eye field results in curved saccades. *J Neurophysiol* 96: 2699–2711, 2006.
- McPeck RM, Han JH, Keller EL. Competition between saccade goals in the superior colliculus produces saccade curvature. *J Neurophysiol* 89: 2577–2590, 2003.
- McPeck RM, Keller EL. Saccade target selection in the superior colliculus during a visual search task. *J Neurophysiol* 88: 2019–2034, 2002.
- McSorley E, Haggard P, Walker R. Distractor modulation of saccade trajectories: spatial separation and symmetry effects. *Exp Brain Res* 155: 320–333, 2004.
- McSorley E, Haggard P, Walker R. Time-course of oculomotor inhibition revealed by saccade trajectory modulation. *J Neurophysiol* 96: 1420–1424, 2006.
- McSorley E, Haggard P, Walker R. The spatial and temporal shape of oculomotor inhibition. *Vision Res* 49: 608–614, 2009.
- Mulckhuyse M, van Zoest W, Theeuwes J. Capture of the eyes by relevant and irrelevant onsets. *Exp Brain Res* 186: 225–235, 2008.
- Munoz DP. Commentary: saccadic eye movements: overview of neural circuitry. *Prog Brain Res* 140: 89–96, 2002.
- Munoz DP, Everling S. Look away: the anti-saccade task and the voluntary control of eye movement. *Nat Rev Neurosci* 5: 218–228, 2004.
- Port NL, Wurtz RH. Sequential activity of simultaneously recorded neurons in the superior colliculus during curved saccades. *J Neurophysiol* 90: 1887–1903, 2003.
- Saslow MG. Effects of components of displacement-step stimuli upon latency for saccadic eye movement. *J Opt Soc Am A* 57: 1024–1029, 1967.
- Schall JD, Thompson KG. Neural selection and control of visually guided eye movements. *Annu Rev Neurosci* 22: 241–259, 1999.
- Schlag-Rey M, Schlag J, Dassonville P. How the frontal eye field can impose a saccade goal on superior colliculus neurons. *J Neurophysiol* 67: 1003–1005, 1992.
- Sheliga BM, Craighero L, Riggio L, Rizzolatti G. Effects of spatial attention on directional manual and ocular responses. *Exp Brain Res* 114: 339–351, 1997.
- Sheliga BM, Riggio L, Rizzolatti G. Orienting of attention and eye-movements. *Exp Brain Res* 98: 507–522, 1994.
- Sheliga BM, Riggio L, Rizzolatti G. Spatial attention and eye-movements. *Exp Brain Res* 105: 261–275, 1995.
- Sommer MA, Wurtz RH. Composition and topographic organization of signals sent from the frontal eye field to the superior colliculus. *J Neurophysiol* 83: 1979–2001, 2000.
- Theeuwes J. Perceptual selectivity for color and form. *Percept Psychophys* 51: 599–606, 1992.
- Theeuwes J, de Vries GJ, Godijn R. Attentional and oculomotor capture with static singletons. *Percept Psychophys* 65: 735–746, 2003.
- Theeuwes J, Godijn R. Inhibition-of-return and oculomotor interference. *Vision Res* 44: 1485–1492, 2004.
- Theeuwes J, Kramer AF, Hahn S, Irwin DE. Our eyes do not always go where we want them to go: capture of the eyes by new objects. *Psychol Sci* 9: 379–385, 1998.
- Theeuwes J, Van der Burg E. The role of spatial and non-spatial information in visual selection. *J Exp Psychol Hum Percept Perform* 33: 1335–1351, 2007.
- Thompson KG, Bichot NP. A visual saliency map in the primate frontal eye field. *Prog Brain Res* 147: 251–262, 2005.
- Thompson KG, Bichot NP, Sato TR. Frontal eye field activity before visual search errors reveals the integration of bottom-up and top-down saliency. *J Neurophysiol* 93: 337–351, 2005.
- Tipper SP, Howard LA, Paul MA. Reaching affects saccade trajectories. *Exp Brain Res* 136: 241–249, 2001.
- Trappenberg TP, Dorris MC, Munoz DP, Klein RM. A model of saccade initiation based on the competitive integration of exogenous and endogenous signals in the superior colliculus. *J Cogn Neurosci* 13: 256–271, 2001.
- Van der Stigchel S, Meeter M, Theeuwes J. Eye movement trajectories and what they tell us. *Neurosci Biobehav Rev* 30: 666–679, 2006.
- Van der Stigchel S, Theeuwes J. Relation between saccade trajectories and spatial distractor locations. *Cogn Brain Res* 25: 579–582, 2005.
- Van der Stigchel S, Theeuwes J. Our eyes deviate away from a location where a distractor is expected to appear. *Exp Brain Res* 169: 338–349, 2006.
- van Zoest W, Donk M. The effects of saliency on saccadic target selection. *Vis Cogn* 2: 353–375, 2006.
- van Zoest W, Donk M. Saccadic target selection as a function of time. *Spat Vis* 19: 61–67, 2005.
- van Zoest W, Donk M, Theeuwes J. The role of stimulus-driven and goal-driven control in saccadic visual selection. *J Exp Psychol Hum Percept Perform* 30: 746–759, 2004.
- Walker R, McSorley E. The influence of distractors on saccade target selection: saccade trajectory effects. *J Eye Mov Res* 2: 1–13, 2008.
- Walker R, McSorley E, Haggard P. The control of saccade trajectories: direction of curvature depends on prior knowledge of target location and saccade latency. *Percept Psychophys* 68: 129–138, 2006.